Evolution: Velvet worm biogeography

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The present-day distribution of velvet worms corresponds neatly to the ancient supercontinent Gondwana – except for a puzzling outpost in southeast Asia. Jaw-dropping new fossil material now establishes when and how peripatid onychophorans reached this isolated spot.

Being quick to desiccate, slow to move, and very particular about habitat, velvet worms do not make natural globetrotters. This diminutive phylum has nevertheless established itself in temperate and tropical forests the world around. The distribution of modern onychophorans largely corresponds to the ancient assembly of South Africa, Africa and Australia into the southern supercontinent Gondwana – except for a small population domiciled in southeast Asia. Could this isolated lineage have dwelt on a fragment of the Gondwanan supercontinent as it drifted across the ocean and collided with the northern supercontinent Laurasia – or does the enclave represent the diminished remnant of a once extensive Laurasian population? A new study of spectacular hundred million year old fossils provides a palaeontological perspective on this puzzling question [1].

Though Onychophora is today a small phylum of under 200 principally endemic species, its evolutionary history is rich and fascinating. The first components of the velvet worm body plan can be recognized in exceptionally preserved Cambrian fossils, identifying an eclectic group of these 500 million year old organisms as early (stem-group) onychophorans [2–4]. Molecular clocks indicate that velvet worms made their way onto land in the Devonian (c. 400 Ma), just as the first forests were becoming established [5]. A distinctively modern body organization is already recognizable in the first fossils of terrestrial onychophorans (c. 300 Ma) [6], and scarcely changes thereafter: the only morphological distinction between the two extant families is the position of their genital openings and the detailed construction of their jaws [6].

Geographically, however, each family has a distinct distribution that corresponds to a contiguous region of the ancient supercontinent Gondwana, which fragmented from 150–100 Ma [7]: the austral distribution of Peripatopsidae corresponds the temperate climate belt of Gondwana, whereas the extent of Peripatidae largely corresponds to the Gondwanan (and modern) tropics [8] (see figure). An intriguing further population in southeast Asia, whose members represent the sister group to all other peripatids [9], has previously been interpreted as arriving around 65–55 Ma with the Indian subcontinent, which separated from Gondwana around 130 Ma [10].

De Sena Oliveira and colleagues now discount this possibility by documenting an Asian peripatid, *Cretoperipatus burmiticus*, from 100 million year old Burmese amber [1]. Living as they do in hotbeds of decay, merely surviving as a fossil is enough for an onychophoran to capture the attention of palaeontologists. What is more, with doubt being cast on the attribution of other onychophoran-like fossils in amber [6,11], *Cretoperipatus* may transpire to be the only fossil of its type. And the claustration of the unfortunate worms in tree resin, now fossilized as amber, has preserved exquisite detail: the synchrotron tomographic renderings produced by de Sena Oliveira and colleagues rival electron micrographs of modern material in both resolution and clarity [1], and have to be seen to be believed. It is not only the fidelity of this ancient species that approximates a modern onychophoran: by adding three new specimens to the one partial fragment previously known [12], the authors show that every pad, papilla and tubercle in *Cretoperipatus* corresponds precisely in position to those in the sole extant Indian onychophoran *Typhloperipatus williamsoni*. This close correspondence extends to the jaws, claws, and antennae; if not for the absence of eyes in *T. williamsoni*, the modern and fossil material could almost be conspecific. More broadly, *Cretoperipatus* shares a number of features with the southeast Asian peripatids, marking the extinct and extant representatives of this geographically proximal group as closely related. By extending the presence of this population back to the Cretaceous, the authors establish that onychophorans reached southeast Asia before India did – discounting the subcontinent as a vector for onychophoran dispersal.

This raises the question of how a taxon as sedentary as Onychophora covered this great distance. Floating rafts of vegetation or soil can disperse rather unlikely taxa [13], but such a mechanism is difficult to reconcile with onychophorans' intolerance of salt water [14] and preference for high humidity [15]. Indeed, the non-overlapping ranges of Peripatidae and Peripatopsidae identify vicariance rather than dispersal as the key control on onychophoran biogeography.

De Sena Oliveira and colleagues [1] propose that African peripatids were transported to Eurasia by the Apulia microplate, which drifted from Gondwana to Europe early in the Cretaceous period [16]. This scenario would sit most easily if Asian peripatids were the closest relatives of African populations – but on the contrary, molecular phylogenetic results [9] indicate that the southeast Asian lineage diverged before the division of the African and South American populations. Indeed, the separation of the Asian onychophorans is dated to somewhere between the Devonian and Triassic (95% probability interval = 360–210 Ma) [9], long before either Apulia or South America split from Africa – making it difficult to reconcile plate tectonic reconstructions with the molecular clock in this scenario.

Each of these possibilities assumes that the southeast Asian lineage has its roots in Gondwana. An alternative is that onychophorans were already present on Laurasia before it split from Gondwana c. 150 million years ago [9]. Even if the identity of candidate 'onychophorans' from Laurasian amber is in dispute [1,6], *Cretoperipatus* happens to strengthen the case that the 300 million year old Laurentian fossil *Helenodora* is an onychophoran by establishing that its apparent lack of claws and slime papillae [17] can be explained by preservational processes [1]. The recent description of the French onychophoran fossil *Antennipatus* [6] further indicates that terrestrial onychophorans inhabited Laurentia during the Carboniferous. *Cretoperipatus* [1] bridges the temporal gap between these early onychophorans and the surviving Asian population; if a passage through India or Eurogondwana can be dismissed, it demonstrates the continued presence of peripatids on Laurentia since the continent split from Gondwana.

This raises the possibility that onychophorans first arose on Laurasia, rather than Gondwana. Though it would be naïve to interpret any living group as directly representing an ancestral population, the molecular data – only being available from a single Asian taxon [9] – do leave open the intriguing possibility that Asian peripatids could be paraphyletic to the rest of Peripatidae. On this view, the morphological features that de Sena Oliveira and colleagues recognize as uniting living and fossil Asian peripatids [1] might even represent the ancestral peripatid condition, rather than synapomorphies of a modern clade.

Whichever continent ultimately gave rise to the peripatids, the new Cretaceous material hints at a much wider distribution than is immediately apparent from present day occurrences. Perhaps – given the extreme morphological similarity between the fossil and modern forms, documented in such detail through the spectacular imaging of these remarkable fossils – modern onychophorans provide a good proxy for the climatic and habitat preferences of their antecedents. Modeling how climate, humidity and vegetation patterns changed as Eurasia rotated through the Mesozoic would offer an interesting approach to evaluating possible trends in onychophoran distribution, particularly as the Laurasian peripatids retreated to their present position on Eurasia's southern fringe. Further fossil finds will be necessary to establish whether the range of peripatopsids also extended beyond its present limit. But whatever fate befell their compatriots, and however they reached their current home, the onychophorans living today in southeast Asia can now be recognised as the last bastion of an ancient lineage that has remained morphologically stable for at least 100 million years.

References

[1] de Sena Oliveira I, Bai M, Jahn H, Gross V, Martin C, Hammel JU, et al. The oldest velvet worm in amber reveals early migration patterns of Gondwanan onychophorans into Southeast Asia. Curr Biol 2016.

[2] Smith MR, Ortega-Hernández J. *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. Nature 2014;514:363–6. doi:10.1038/nature13576.

[3] Yang J, Ortega-Hernández J, Gerber S, Butterfield NJ, Hou J-B, Lan T, et al. A superarmored lobopodian from the Cambrian of China and early disparity in the evolution of Onychophora. Proc Natl Acad Sci USA 2015;112:8678–83. doi:10.1073/pnas.1505596112.

[4] Zhang X-G, Smith MR, Yang J, Hou J-B. Onychophoran-like musculature in a phosphatized Cambrian lobopodian. Biol Lett

[5] Rota-Stabelli O, Daley AC, Pisani D. Molecular timetrees reveal a Cambrian colonization of land and a new scenario for ecdysozoan evolution. Curr Biol 2013;23:392–8. doi:10.1016/j.cub.2013.01.026.

[6] Garwood RJ, Edgecombe GD, Charbonnier S, Chabard D, Sotty D, Giribet G.

Carboniferous Onychophora from Montceau-les-Mines, France, and onychophoran terrestrialization. Invertebr Biol 2016. doi:10.1111/ivb.12130.

[7] Seton M, Müller RD, Zahirovic S, Gaina C, Torsvik T, Shephard G, et al. Global continental and ocean basin reconstructions since 200Ma. Earth-Science Rev 2012;113:212–70. doi:10.1016/j.earscirev.2012.03.002.

[8] Monge-Nájera J. Phylogeny, biogeography and reproductive trends in the Onychophora. Zool J Linn Soc 1995;114:21–60. doi:10.1111/j.1096-3642.1995.tb00111.x.

[9] Murienne J, Daniels SR, Buckley TR, Mayer G, Giribet G. A living fossil tale of Pangaean biogeography. Proc R Soc B 2014;281:20132648. doi:10.1098/rspb.2013.2648.

[10] Briggs JC. The biogeographic and tectonic history of India. J Biogeogr 2003;30:381–8. doi:10.1046/j.1365-2699.2003.00809.x.

[11] Poinar G. Fossil onychophorans from Dominican and Baltic amber: *Tertiapatus dominicanus* n.g., n.sp. (Tertiapatidae n.fam.) and *Succinipatopsis balticus* n.g., n.sp. (Succinipatopsidae n.fam.) with a proposed classification of the subphylum Onychophora. Invertebr Biol 2000;119:104–9. doi:10.1111/j.1744-7410.2000.tb00178.x.

[12] Grimaldi DA, Engel MS, Nascimbene PC. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. Am Museum Novit 2002;3361:1–71. doi:10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2.

[13] Longrich NR, Vinther J, Pyron RA, Pisani D, Gauthier JA. Biogeography of worm lizards (Amphisbaenia) driven by end-Cretaceous mass extinction. Proc R Soc London B Biol Sci 2015;282:20143034. doi:10.1098/rspb.2014.3034.

[14] Monge-Nájera J, Barrientos Z, Aguilar F. Experimental behaivour of a tropical invertebrate: *Epiperipatus biolleyi* (Onychophora: Peripatidae). Acta Myriapodologica Mém Mus Natn Hist Nat 1996;169:493–4.

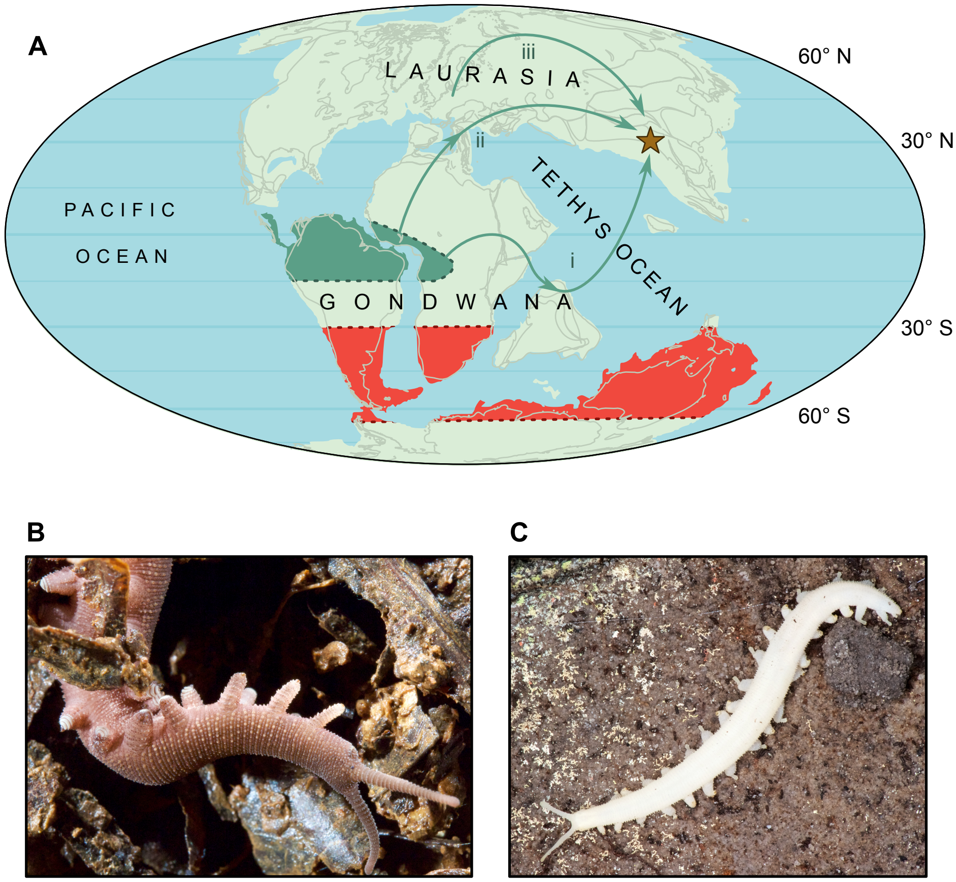
[15] Bursell E, Ewer DW. On the reactions to humidity of *Peripatopsis moseleyi* (Wood-mason). J Exp Biol 1950;26:335–53.

[16] Ezcurra MD, Agnolín FL. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. Syst Biol 2012;61:553–66. doi:10.1093/sysbio/syr115.

[17] Murdock DJE, Gabbott SE, Purnell MA. The impact of taphonomic data on phylogenetic resolution: *Helenodora inopinata* (Carboniferous, Mazon Creek Lagerstätte) and the onychophoran stem lineage. BMC Evol Biol 2016;16:19. doi:10.1186/s12862-016-0582-7.

Figure: Onychophoran biogeography in the Cretaceous

(A) Distribution of continents 100 million years ago [after ref. 7], with indicative ranges of Peripatidae (green) and Peripatopsidae (red) based on a Gondwanan distribution. Star denotes *Cretoperipatus* fossils newly reported by de Sena Oliveira and colleagues [1]. Arrows indicate three proposed provenances of southeast Asian peripatids: (i) India; (ii) Eurogondwana; (iii) Laurasia. (B–C) extant onychophorans *Mesoperipatus tholloni* (Peripatidae) and *Peripatopsis alba* (Peripatopsidae), courtesy Gonzalo Giribet.


A
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TETHYS OCEAN
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